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THE TIFFANY FAUNA, UPPER PALEOCENE

I.—MULTITUBERCULATA, MARSUPIALIA, INSECTIVORA, AND ?CHIROPTERA

BY GEORGE GAYLORD SIMPSON

INTRODUCTION

The Tiffany fauna has become the characteristic or almost classical fauna of the American Upper Paleocene and the name Tiffany has come into wide use for the zone and time represented by the fauna, but it has been described incompletely and in scattered papers or in incidental notes included in work on other subjects. Some of the fossil mammals of the Tiffany have never been named, most of them have never been figured, and only two have been adequately described.

Practically all of the known specimens were collected by Dr. Walter Granger (with Mr. George Olsen) in 1916 and are in the American Museum. As referred to in more detail below, Matthew and Granger have published several notes on the Tiffany and its mammals, but these were for the most part brief and preliminary, and no general review has appeared. It was expected that Doctor Matthew would take up the definitive study in conjunction with his revision of the Puerco and Torrejon, but at the time of his death in 1930 he had not yet undertaken the Tiffany study and except for brief mention and the description of one new species it is omitted from the manuscript which he left.

As I am engaged in a revision of the Montana Fort Union fauna and have in this connection and in others had occasion to familiarize myself with the Tiffany fauna, Doctor Granger has now placed it in my hands and requested that I complete the description which he and Doctor Matthew so ably began. One manuscript diagnosis, that of *Periptychus superstes* Matthew, was available and has been directly quoted below.

The present paper contains the introductory material, résumés, and the orders Multituberculata, Marsupialia, Insectivora, and ?Chiroptera. A second paper will be devoted to *Plesiadapis* and a third to the remainder of the fauna. References are given at the end of the third paper. The drawings in all three papers are by Mrs. Mildred Clemans.

PREVIOUS WORK

The formation (or faunal zone) later designated as Tiffany was discovered by J. W. Gidley in 1909. He then visited southwestern Colorado with J. H. Gardner, of the U. S. Geological Survey, and found a few fragmentary mammals later tentatively identified as follows.[1]

Coryphodon.[2]

Phenacodont intermediate between *Phenacodus* and "*Euprotogonia*" [= *Tetraclaenodon*].

Hemiacodon[2] (?sp. nov.).

"*Nothodectes*" sp. [= *Plesiadapis*].

He concluded that the fauna is intermediate between the Fort Union or Torrejon and the Wasatch.

On information received from Gidley, Granger examined these beds in 1916. He then made the collection which is the subject of the present revision and published an account of the stratigraphy, with notes on the fauna (Granger 1917). He applied the name Tiffany Beds to the horizon of these fossils and tentatively correlated it with the Clark Fork. While the preparation of the extremely delicate material by Miss Erna Kohlhaase was in progress, Matthew (1917*a*, 1917*b*) published preliminary descriptions of *Zanycteris paleocena* and "*Nothodectes*" *gidleyi*. A few years later, Matthew and Granger (1921) published brief, unillustrated diagnoses of the following Tiffany genera and species: *Ectypodus musculus*, *Peradectes elegans*, *Leptacodon tener*, *Xenacodon mutilatus*, *Labidolemur soricoides*, *Ignacius frugivorus*, *Navajovius kohlhaasae*, and *Carpodaptes aulacodon*. *Ectypodus musculus* was figured and more fully described by Granger and Simpson (1929). In connection with work on other Paleocene faunas, a number of students have examined this incompletely published Tiffany collection, and papers by Jepsen, Russell, Simpson, and others contain references to it, or involve unpublished observations on it, but no studies other than those cited above are directly descriptive of it. Although a few fragments, not adding to knowledge of the fauna, have been picked up in passing, there has not been, to the best of my knowledge, any intensive collecting in the Tiffany since 1916, and the collection of that season remains practically the whole basis for knowledge.

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[1] Gidley, 1917 (a brief note inserted in a paper by C. H. Wegemann).

[2] These generic determinations are probably erroneous, or the fossils were from a higher horizon. The specimens were very fragmentary and have been lost or discarded.

OCCURRENCE

The occurrence of the Tiffany fauna has been described by Granger (1917) and the following is abstracted from his more extended account: The area in question is in southwestern Colorado, near the boundary with New Mexico, on the northern drainage slope of the San Juan River, and is included in an arc on which lie the settlements or stations Ignacio, Tiffany, Arboles, and Pagosa Junction. Granger's map shows nine fossil localities, the most distant about ten miles apart, on the valley slopes facing Spring Creek on the west, the San Juan River on the south, and on the two sides of the Piedra River valley, which runs southward to the San Juan through the middle of this area. The great majority of the specimens, however, are from a limited area in the most western of the fossiliferous exposures, four to five miles north of the station of Tiffany, in Sec. 20, T. 33 N., R. 6 W.

As regards occurrence, the fossils fall into two categories. A few, for the most part the larger animals of the fauna, were found isolated at scattered localities. Many, exclusively small to minute animals, were found in a single small pocket of gray shale imbedded in a stratum of mottled purplish and brownish clay. "This gray shale mass was irregular in shape and less than half a cubic yard in bulk, although probably considerably reduced by erosion, and having all the appearance of being the filling of a fissure formed in the mottled clay. . . . The fossils are rather evenly distributed through the matrix. . . . The occurrence of so many small forms in this deposit and the absence of any of the larger ones suggests that they may be the remains of animals brought into a fissure by a small predatory animal" (Granger 1917, pp. 827–828). The fossils found in this pocket, called the Mason Pocket by Granger from the nearby Mason schoolhouse, and those found elsewhere are listed separately below.

FAUNAL LIST

The Tiffany fossils so far identified are here listed, with the number of specimens of each found in the Mason Pocket and elsewhere.[1]

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[1]The exact number of individuals in the Mason Pocket cannot be determined. The mass contained quantities of isolated bones and teeth, but I have not included them in the numbers given unless they were characteristic and fully identifiable.

Name	Mason Pocket	Elsewhere
MULTITUBERCULATA		
Ptilodontidae		
Ectypodus musculus	12 +	
MARSUPIALIA		
Didelphidae		
Peradectes elegans	20	
INSECTIVORA		
Leptictidae		
Leptacodon tener	2	
Xenacodon mutilatus	1	
?CHIROPTERA		
?Phyllostomatidae		
Zanycteris paleocena	1	
PRIMATES		
Plesiadapidae		
Plesiadapis gidleyi	20 +	1
Apatemyidae		
Labidolemur soricoides	2	
Carpolestidae		
Carpodaptes aulacodon	1	
Anaptomorphidae		
Navajovius kohlhaasae	3	
Family uncertain		
Phenacolemur frugivorus	7	
CARNIVORA		
Arctocyonidae		
Chriacus sp.		1
Thryptacodon australis	1	
Mesonychidae		
?*Dissacus* sp.		1
CONDYLARTHA		
Phenacodontidae		
Phenacodus grangeri		9
Phenacodus matthewi		1
Phenacodus gidleyi		1
Phenacodus sp.		1
AMBLYPODA		
Periptychidae		
Periptychus superstes		5
TOTALS:	70 +	20

FACIES

It is evident that the facies of the Mason Pocket is very peculiar, and the marked difference between this and the rest of the formation demonstrates that strata may be identical in age and yet have remarkably different faunas.[1] The fauna of the formation outside the pocket, while scanty, seems quite usual and is comparable in facies to that of the great majority of Tertiary deposits, predominantly ungulates, with a few carnivores. It is evidently a normal terrestrial fauna and the deposits are those of flood plains.

In the pocket there are no ungulates and only one carnivore, of small size, and the great majority of the fossils represent minute animals of groups elsewhere very rare. Several specimens of *Plesiadapis* have now been found at other American localities, but it is still rare elsewhere. *Peradectes* has not been found at any other locality, and only one other specimen of a didelphid has ever been encountered in the whole American Paleocene. Multituberculates are common in some other deposits, but, especially the small and delicate forms, seldom make up such a large percentage of the fauna (at least 17 per cent). Several of the animals rare here are quite unknown elsewhere.

A full explanation of the peculiarity is impossible, but it seems clear that the majority of the Mason Pocket animals, and perhaps all of them, are arboreal. *Plesiadapis* can be designated as arboreal with little question, its skeleton having very numerous characters usually associated with such a station. With the other genera, judgment must be based more largely on inference, but it is very probable that the small multituberculate, the *Marmosa*-like marsupial, and all the primates were also arboreal. The other groups, leptictids, ?bat, and small carnivore may well have been arboreal also. In Tertiary deposits in general arboreal mammals are rare, and this characterizes the difference of facies, although of course it does not explain just how it happened that arboreal animals were preserved in this case and are so rare elsewhere.

A typical collection of mammals from a coal mine at Bear Creek, Montana, contains the following numbers of identified individuals.

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[1]Incidentally, it once more exposes the fallacy of "percentage correlation," often criticized but still popular in some quarters. Of fifteen species definitely identified, one, or less than 7 per cent of the combined fauna, is common to the Mason Pocket and the other facies of the formation. If they were not known to be of the same age, this fallacious means of correlation would separate them very widely.

INSECTIVORA	
Plagiomenidae	
Planetetherium mirabile	29 +
Nyctitheriidae	
Protentomodon ursirivalis	5
?Pantolestidae	
?*Pentacodon* cf. *inversus*	2
Leptictidae	
Leptacodon siegfriedti	10
PRIMATES	
Plesiadapidae	
Plesiadapis sp.	1
Apatemyidae	
Labidolemur kayi	1
Carpolestidae	
Carpolestes nigridens	3
Carpolestes aquilae	3
TAENIODONTA	
Stylinodontidae	
?*Psittacotherium lobdelli*	2
CARNIVORA[1]	
Arctocyonidae	
Thryptacodon pseudarctos	2
CONDYLARTHRA	
Phenacodontidae	
Phenacodus cf. *primaevus*	1

This fauna is of about the same age as that of the Tiffany and has five genera in common with the latter and another (*Carpolestes*) very nearly allied (to *Carpodaptes*), yet it is evidently of very different facies. *Plesiadapis* is abundant in the Mason Pocket, very rare at Bear Creek; *Leptacodon* is common at Bear Creek, rare in the Mason Pocket; and so on. But still more striking is the total absence at Bear Creek of any allies of two of the commonest Mason Pocket fossils, *Ectypodus* and *Peradectes*, while far the most common Bear Creek genus, *Planetetherium*, has no ally in the Tiffany fauna. The Bear Creek fauna seems also to include arboreal elements, although less exclusively arboreal in nature, and the difference must be sought in other factors of environment or of mode of deposition of the fossil beds. On the former score, the more northern locality may have some bearing on climate and on both the fact that the Bear Creek fossils are found in immediate proximity to a coal seam is almost surely significant.

[1]There are several other creodonts, but their remains are too fragmentary for identification.

AGE

Gardner (in Lee, 1912) included the then unnamed Tiffany Beds and the overlying thick barren series in the "Wasatch," in default of clear fossil evidence. Gidley (in Wegemann, 1917), on the basis of the few fossils then known to him, considered the fauna as intermediate between the Fort Union and the Wasatch, or, to paraphrase his words and make his meaning more clear in present terminology, between the Torrejon and the Gray Bull, a conclusion now considered beyond question. Granger (1917) reached the same conclusion (expressed in slightly different words) and suggested that "the closest correlation . . . seems to be with the Clark Fork beds of Wyoming." Regarding the quite different question as to where the Paleocene-Eocene line should be drawn, Granger was then (1917) inclined to draw it below the Tiffany and Clark Fork, and Matthew above them. This of course involves no difference of opinion as to the position of these horizons in the sequence. This view, with numerous differences as to the Paleocene-Eocene line, remained practically unchallenged, and indeed the Tiffany, in spite of inadequate publication of its fauna, came to be considered and used more or less as the standard Upper Paleocene. Differences between Tiffany and Clark Fork were noted, and comparisons made separately, but it was not known whether these indicated a measurable age difference or were entirely facial. I suggested (Simpson 1929), very tentatively, that the Clark Fork might be slightly later. This was confirmed and the known or suspected sequence of the four known Paleocene faunas placed beyond question by Jepsen's discovery (1930) of a continuous series in which equivalents of all of them occur, as follows.

Clark Fork
Tiffany
Torrejon
Puerco[1]

As the Tiffany and Clark Fork are more nearly related to each other than are any other two successive members of this series, they are commonly considered as Upper Paleocene, the Middle and Lower Paleocene including the Torrejon and Puerco, respectively, with their equivalents.

[1]This incidentally established (with great probability) the presence of a Puerco equivalent in the northern area. It had been supposed that the Puerco occurred there, but no fossils had been found to prove this, and the non-mammal-bearing beds in which it would necessarily be included if present were, and in most areas still are, distributed between the Fort Union and the Lance on no very clear criteria by various authors.

The sequence and the position of the Tiffany in it are thus established as exactly as may be, until other possible intermediate horizons are discovered. The Tiffany-Clark Fork-Sand Coulee series seems to be almost completely transitional, so that no intercalation is here probable, but another faunal zone may well be discovered between the Puerco and the Torrejon and between the Torrejon and the Tiffany as now known.

Other Tiffany equivalents had already been recognized, before Jepsen's discovery of the full sequence, in the Paskapoo of Alberta (Simpson, Russell) and in the Fort Union at Bear Creek, Montana (Simpson). The fifteen genera now recognized in the Tiffany (*sensu stricto*) are distributed as follows in time.

	Torrejon	Tiffany (and equivalents)	Clark Fork	Lower Eocene
Ectypodus	?	×		
Peradectes		×		
Leptacodon		×		
Xenacodon		×		
Zanycteris		×		
Plesiadapis		×	×	?
Labidolemur		×		
Carpodaptes		×		
Navajovius		×		
Phenacolemur		×	×	×
Chriacus	×	×		×
Thryptacodon		×	×	×
Dissacus	×	?	×	×
Phenacodus		×	×	×
Periptychus	×	×		

Many of the small mammals have little bearing on age relationships, as the phyla to which they belong are not known in either earlier or later beds. *Plesiadapis* is more advanced than its Torrejon forerunner, *Pronothodectes*, and somewhat (but less markedly) less advanced than Clark Fork-Lower Eocene species placed, at least tentatively, in the same genus. *Labidolemur* is replaced in the Lower Eocene by *Teilhardella;* no Clark Fork representative of this phylum is yet known. *Carpodaptes* is more advanced than its probable ancestor *Elphidotarsius* of Torrejon age, and slightly more primitive than *Carpolestes* with which it is, nevertheless, nearly or quite contemporaneous. The Tiffany representative of the *Phenacolemur* group may be somewhat more primitive than the Clark Fork and later species, but this is not wholly clear. The

creodonts are rather inconclusive, but the *Thryptacodon* seems to be about as advanced as the later species, and no closely similar form is known in the Torrejon. The condylarths, as far as can be exactly determined, are of primitive Eocene, rather than Middle Paleocene, type. *Periptychus* is the only distinctly Middle Paleocene element, and as a survival it is less important than are the more progressive lines as an indication of time relationships.

The Tiffany fauna thus is intermediate in character between the Torrejon and the Clark Fork and Lower Eocene faunas, as universally recognized, but its affinities are preponderantly with the known later faunas, and it very possibly stands nearer even to the unquestioned Eocene Sand Coulee[1] and Gray Bull in time than it does to the Torrejon. By this I do not mean to imply that it should be united with the Eocene and excluded from the Paleocene. That is a question which should, I think, be decided on other criteria. The suggestion is only that there is at present a gap in our knowledge of Paleocene faunas between the Torrejon and the Tiffany. Anticipating conclusions, the basis for which cannot be given here, I believe that the boundary in our essentially continuous Paleocene-Eocene stratigraphic series is more conveniently and naturally drawn above the Clark Fork than below the Tiffany, and certainly there is yet little or no good evidence for drawing it between Tiffany and Clark Fork.

Since the Upper Paleocene, as here defined, was recognized, it has been generally agreed that the French Cernaysian, or the Thanetian of which it is a local facies, is approximately equivalent to the Tiffany or Clark Fork or both. The evidence (see, e.g., Teilhard 1921, Simpson 1929*c*) need not be reviewed in any detail, but the close similarity of a few mammals, *Plesiadapis*, *Thryptacodon-Arctocyonides*, and one or two others, and, still more, the similar relationships to the overlying true Lower Eocene, Gray Bull and Sparnacian, are quite convincing. It is also probable that the Asiatic Gashato and possible that the South American Río Chico are approximate equivalents of the Tiffany, but in these cases the evidence is still less direct and the correlation still very uncertain.

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[1]Abel (1931) calls the Sand Coulee Paleocene, but this is perhaps a *lapsus*, as I know of no American student of its fauna who does not consider it as Eocene. Jepsen even unites it with the Gray Bull

REVISION OF FAUNA
MULTITUBERCULATA

PTILODONTIDAE

Ectypodus musculus Matthew and Granger, 1921

This genus and species have been described in detail by Granger and Simpson (1929, pp. 652–656), and it seems unnecessary to repeat the description. The only dubious point is the presence or absence of P_3. Matthew and Granger stated that this tooth was absent. Granger and Simpson, influenced by the presence of a large basal notch on P_4 and obscure signs of what might be an alveolus stated that it may have been present. There are four specimens in which the region of P_3 is shown. In one, least well preserved here, there might be an alveolus, and in the other three there apparently is none. In spite of the notch in P_4 apparently for the reception of P_3, the presence of the latter tooth is highly dubious. The propriety of maintaining *Parectypodus* Jepsen as distinct is thus in question, depending certainly only on the reduction of the notch of P_4, but it may prove to be more distinctive when upper teeth are known.

MARSUPIALIA

DIDELPHIDAE

PERADECTES Matthew and Granger, 1921

TYPE.—*P. elegans* Matthew and Granger.

DISTRIBUTION.—Tiffany, Colorado.

DIAGNOSIS.[1]—Primitive and generalized didelphines. Dental formula $\frac{?\ .1.3.4.}{?4.1.3.4.}$ Canine moderate, P_1 very small, apparently with only one root. $P\frac{2}{2}$ slightly larger than $P\frac{3}{3}$. M^{1-3} trigonal, paracones nearly as large as metacones, broad outer shelf, five distinct stylar cusps of nearly equal size, proto- and metaconules distinguishable but vestigial, no basal cingula on protocone. M_4 reduced, transverse, paracone slightly larger than metacone. Lower molars of completely didelphine pattern. Trigonids elevated, paraconids distinctly higher than entoconids. M_4 as long as M_3 but narrower and heel reduced.

Some of the characters of this genus were mentioned incidentally by me in a previous note (Simpson 1928) and outline drawings of some parts given. In all its characters the genus is extraordinarily like recent opossums, and especially the various dimunitive species of *Marmosa*,

[1] Modified from Matthew and Granger.

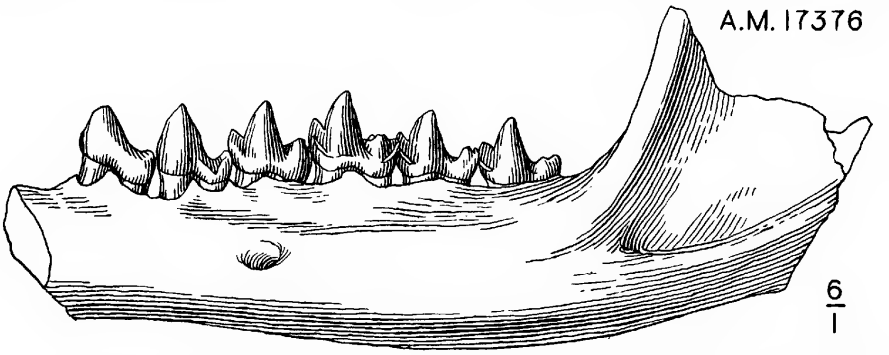

Fig. 1. *Peradectes elegans* Matthew and Granger. Type, Amer. Mus. No. 17376. Left lower jaw with P_2–M_4. External view. Enlarged six diameters.

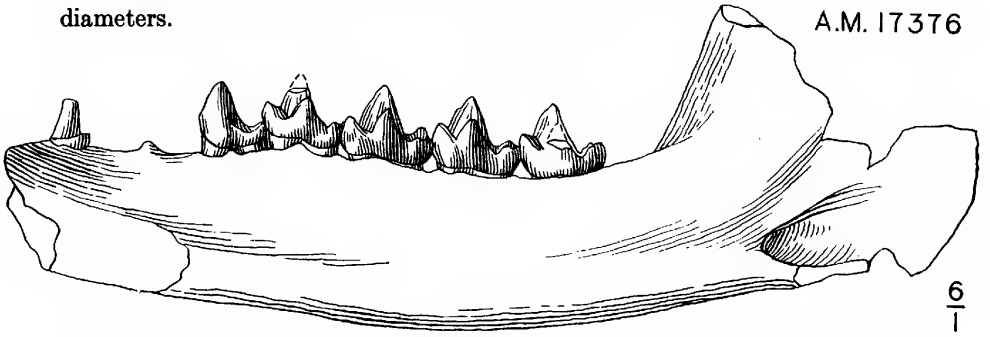

Fig. 2. *Peradectes elegans* Matthew and Granger. Type, Amer. Mus. No. 17376. Right lower jaw with P_1 and P_3–M_4. Internal view. Enlarged six diameters.

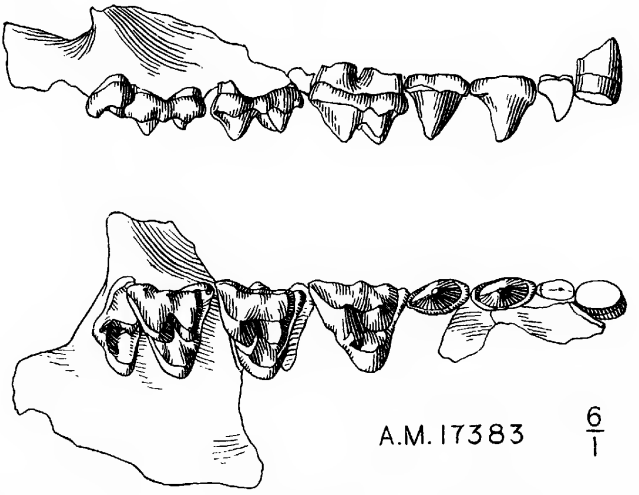

Fig. 3. *Peradectes elegans* Matthew and Granger. Amer. Mus. No. 17383. Right upper jaw with C and P^2–M^4, with P^1 (in outline) supplied from Amer. Mus. No. 17382. External and crown views. Enlarged six diameters.

and is an ideal structural ancestor with the doubtful exception of the greater reduction of P_1. The most noteworthy other distinctions are the less differentiated stylar cusps, less reduced paracones, and more elevated trigonids of the Paleocene genus.

The upper incisors are unknown. The canine is a slender, moderately large, vertically implanted tooth, very much as in *Marmosa*. There are no diastemata in the upper maxillary series. P^1 is a very simple, two-rooted tooth, laterally compressed, with a minute posterior but no anterior basal cuspule. P^{2-3} are subequal but P^2 slightly larger, strongly compressed and trenchant, with anterior and posterior basal cuspules, and surrounded by a basal cingulum which is, however, weaker and inconstant on P^2. The enlargement of $P\frac{2}{2}$ relative to $P\frac{3}{3}$ is characteristic of modern didelphids (although not invariable in *Marmosa*), but is generally absent in the Eocene to Miocene *Peratherium*, and it is interesting to see it established in this very ancient genus, if only in barely noticeable, incipient fashion.

The upper molars are very like those of *Marmosa* except for the details already mentioned. On M^1 the third (middle) stylar cusp is usually slightly highest. On M^2 the second to fourth are nearly equal, the third may be very slightly highest or may be a little lower than the second and fourth. On M^3 the third seems to be constantly smaller than the subequal second and fourth. M^4 has a strong parastylar spur, terminating in a style, and there may be two vague and minute styles on the sharp outer margin as it runs to the metacone.

Amer. Mus. No. 17403 has three small incisors. Although no other is preserved, it may be assumed with great probability that there were four and that these are I_{2-4}. I_{2-3} are subequal and have low, blunt, spatulate crowns. I_4 is not well seen, but appears to be much smaller. The lower canine, like the upper, is very suggestive of *Marmosa*. P_1 is a very small tooth, apparently with only one root: the only suggestion of aberrant specialization in the genus (and such a character may not be of more than specific value). P_{2-3} are compressed, trenchant teeth with elevated anterior cusps, that of P_3 about as high as the protoconid of M_1, and that of P_2 very slightly higher. Each has a low, one-cusped posterior heel. On P_2 the posterior trenchant crest curves more directly to the posterior basal point while on P_3 a more distinct notch cuts off the larger talonid cuspule from the main part of the tooth. The lower molars are so simple and thoroughly didelphine as to require no further notice.

Part of the palate is preserved, very poorly, in one specimen but it shows nothing of special interest beyond a generally *Marmosa*-like character (fenestration present but size and shape not determinable). The mandible also appears to be as in the more delicate species of *Marmosa*. The relatively large posterior mental foramen is beneath M_1. The position of the anterior foramen cannot be determined.

Peradectes elegans Matthew and Granger, 1921

TYPE.—Amer. Mus. No. 17376, pair of lower jaws with right P_1 and P_3–M_4 and left P_2–M_4.

PARATYPE.—Amer. Mus. No. 17369, left M^{1-4}.

HORIZON AND LOCALITY.—Mason Pocket, Tiffany Beds, Colorado.

DIAGNOSIS.—Sole known species of genus. Measurements are given below.

P_1–M_4 (type): 10.8 mm.
M_1–M_4 (type): 6.2 mm.
P^1–M^4 (Amer. Mus. No. 17382): about 10.5 mm.
M^1–M^4 (paratype): 5.3 mm.
M^1–M^4 (Amer. Mus. No. 17382): about 5.7 mm.

INSECTIVORA

LEPTICTIDAE

LEPTACODON Matthew and Granger, 1921

TYPE.—*L. tener* Matthew and Granger.

DISTRIBUTION.—Tiffany, Colorado. Fort Union, "Princeton Quarry Level," Park County, Wyoming. Bear Creek, Montana.

DIAGNOSIS.[1]—P_4 with small metaconid, high on crown, partly connate with protoconid, paraconid low but as strong as on molars, talonid small, narrow, internal. Molar trigonids less elevated than in *Diacodon*, paraconids distinct but small, internal. Heel of M_3 with three subequal cusps, hypoconulid projecting but not excluded from basin. Protoconids nearly equal to metaconids, or slightly higher. Lower molars reduced in size from first to third.

This is a typically leptictine genus differing from *Diacodon* only in minute details, notably the slightly less progressive P_4 with smaller heel, less elevated molar trigonids, more internal paraconids, and shorter and simpler heel of M_3.

In 1928 I described *Leipsanolestes siegfriedti* from Bear Creek, Montana, comparing it with the European *Adapisorex*. Discovery of better material and Teilhard's restudy of *Adapisorex* showed that *Leipsanolestes* is more closely related to *Leptacodon* and I later (1929) made

[1]The brief diagnosis by Matthew and Granger was later emended by me (Simpson 1929, p. 118). The present diagnosis is a slight further emendation from further study and the discovery of specimens of the genus at other localities.

it a subgenus of the latter. There is some question as to the propriety of distinguishing genera on such slight differences as those supposedly characterizing *Diacodon*, *Prodiacodon*, and *Leptacodon*, emphasized by the discovery of the variant species *Leptacodon packi* and *Diacodon minutus* by Jepsen. It is unlikely that all these, with *Leptacodon* (*Leipsanolestes*), belong to one genus, but it is by no means clear that the genera are, or can be, now properly defined or that the lines between them are properly drawn.

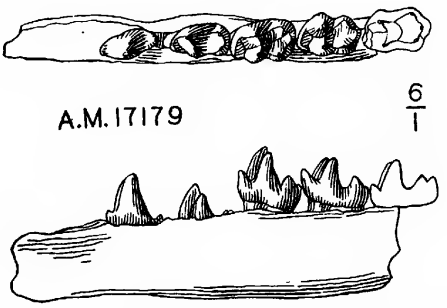

Fig. 4. *Leptacodon tener* Matthew and Granger. Type, Amer. Mus. No. 17179. Right lower jaw with P_3–M_2, with M_3 (in outline) supplied from Amer. Mus. No. 17395. Crown and internal views. Enlarged six diameters.

The slight variation from typical and very well-known leptictid structure and the detailed description of *L. packi* by Jepsen (1930, pp. 510–511) make extended description of the dentition unnecessary.

Leptacodon tener Matthew and Granger, 1921

TYPE.—Amer. Mus. No. 17179, crushed skull and jaws (most parts very obscure but P_3–M_2 well shown).

HORIZON AND LOCALITY.—Mason Pocket, Tiffany, Colorado.

DIAGNOSIS.—Length M_{1-3}, 4.3 mm. Trigonid of P_4 relatively low. Protoconid about equal to metaconid on M_1, slightly lower on M_{2-3}. Hypoconids all slightly larger than entoconids. Hypoconulids projecting, that of M_3 prominently so. Molar cusps slender.

L. tener and *L. packi* are of almost exactly the same size and are so similar that they are not well distinguished, although probably different. Wear, crushing, and differences in individual observation particularly obscure the proper comparison of these small species, and nothing is actually known as to their range of variation. *L. siegfriedti* is also closely similar but is definitely larger and more robust and otherwise seems more distinctive.

XENACODON Matthew and Granger, 1921

TYPE.—*X. mutilatus* Matthew and Granger.

DISTRIBUTION.—Tiffany, Colorado.

DIAGNOSIS.[1]—Dental formula $?3.1.4.3$. Incisors small. Canine small, followed by very short diastema. All premolars two-rooted. P_4 with large metaconid about equal to protoconid, paraconid small, basal, talonid very short and not or very indistinctly basined. On M_{2-3} trigonid less elevated than in *Prodiacodon*, protoconid slightly larger than metaconid; hypoconid large, united in a crest with hypoconulid, entoconid very small, more isolated, and conical. Talonid of M_3 reduced, short and very narrow, hypoconulid not projecting.

The only specimen is of a young individual, with P_4 just being erupted. From the alveoli, dm_3 was either still in place or had been lost a very short time. M_3 is, however, fully erupted and beginning to wear—this late loss of the deciduous teeth is common in leptictids.

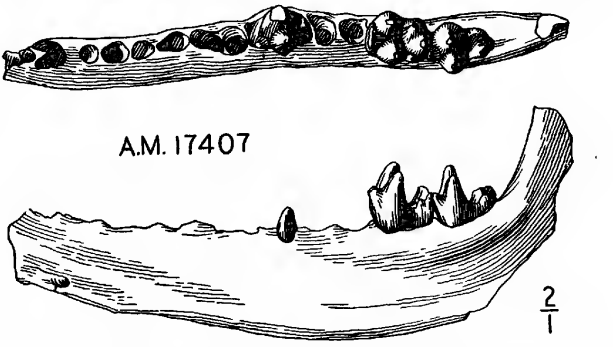

Fig. 5. *Xenacodon mutilatus* Matthew and Granger. Type, Amer. Mus. No. 17407. Right lower jaw with P_4 and M_{2-3}. Crown and internal views. Enlarged six diameters.

The alveoli are obscure, but there were probably three small incisors. P_1 occupied almost as much space as P_2. The transverse heel crest of P_4 seems to have two closely approximated cuspules, but they can hardly be distinguished. The paraconids of M_{2-3} are small, but quite distinct and are about halfway between the primitive anterointernal position and the anteromedian site which they occupy in many more aberrant early mammals. That of M_3 seems to project somewhat more strongly from the trigonid, an unusual character perhaps due only to wear on M_2. The horizontal ramus is very slender, but this may be merely a juvenile character to the extent that it differs from most leptictids. There is a mental foramen beneath P_1 and another, larger, beneath the anterior end of P_3.

[1]Emended from Matthew and Granger.

The general habitus is very leptictid, much like *Prodiacodon* (*"Paleolestes"*), for instance, and there is a definite resemblance in molar structure. This, however, seems to me somewhat less marked than was suggested by Matthew and Granger. The talonids, for instance, are distinctive. Except for being partly molariform, P_4 is very unlike that of any other leptictid. The position of *Xenacodon* in this family is thus not certain, but it is probable and no more satisfactory arrangement is suggested.

Xenacodon mutilatus Matthew and Granger, 1921

TYPE.—Amer. Mus. No. 17407, right lower jaw with P_4, M_{2-3}, and alveoli of the other teeth.

HORIZON AND LOCALITY.—Mason Pocket, Tiffany Beds, Colorado.

DIAGNOSIS.—Sole known species of the genus as defined above. M_2, length 3.5 mm., width 3.1 mm. M_3, length 3.7 mm., width 2.3 mm.

?CHIROPTERA

?PHYLLOSTOMATIDAE

ZANYCTERIS Matthew, 1917

TYPE.—*Z. paleocena* Matthew.

DISTRIBUTION.—Tiffany, Colorado.

DIAGNOSIS.[1]—Dental formula $^{?.1.3.3.}$ Incisors not determinable. Canine small, laterally compressed, with posterior, but no anterior, cutting crest. Canine followed by diastema. Alveoli of each premolar occupying about same space as that of canine, anteroposterior. Alveoli of P^2 confluent, those of P^3 imperfectly separated, those of P^4 distinct, posterior larger. M^1 very large, M^{2-3} progressively much smaller. Molar contour transitional from nearly triangular, M^1, to subquadrate, M^3. Crowns broadly basined with rugose enamel. Paracone, metacone, and protocone distinct but low and marginal save for external cingula. M^{2-3} with hypocone suggested but not distinctly cuspidate. M^1 with anterointernal and large posterointernal cingula. Muzzle narrowing rapidly anterior to molars, elongated. Cranium short and broad. Zygoma probably complete, arising at the junction of M^1 and M^2. Sagittal crest low.

The unique specimen is a nearly complete skull, but so badly crushed that no details can be made out beyond the general shape of the palate and muzzle and the less definite and few additional points mentioned in the diagnosis.

The small canine is not perfectly oval in section, but it is less elongate, less enlarged, and generally much less specialized than in the modern forms of most nearly comparable molar pattern. It is a simple tooth, the crown very slightly procumbent, swollen and oval except for

[1]Slightly modified from Matthew.

a poorly developed posterior vertical crest and a slight excavation on the inner (lingual) side of this. This is followed by a diastema approximately equal to the canine root in length, and then by the three closely spaced premolars, the crowns of which are not preserved.

The very large first molar is subtriangular, but the inner part is rounded out by its cingula so as to form a semicircle inscribing the inner angle of the triangle formed by the protocone. The greater part of the crown is occupied by a broad, shallow basin with markedly rugose or pitted enamel. Protocone, paracone, and metacone are of about equal height, but the protocone is more prominent, being more isolated and with a more expanded base. The paracone and metacone are far apart, being nearly at the extreme angles of the long outer border, but are united by a sharp crest, which waves slightly outward in the middle, suggesting a very vague mesostyle. Less distinct crests run from the protocone to the paracone and to the metacone, but these are depressed near the longitudinal midline, so that the tooth has, rather vaguely, a broad longitudinal median groove. There is a low, distinct style directly anterior to the paracone, and a strong external cingulum which, however, does not cross the outer face of the paracone. This cingulum rises slightly to form a median style[1] and again to form a vaguely double elevation external to the metacone. The protocone is anterior in position, and hence nearer the paracone than the metacone. No internal cingulum crosses its base, but there is a small, basined, anterointernal basal cingulum, and a larger, basined cingulum originating at the tip of the protocone and sweeping around the posterointernal side of the tooth.

M^2 is less triangular, the protocone directly internal to the paracone, and the protocone-metacone ridge curving first posteriorly, then externally, filling out the posterointernal angle but not forming a definite cusp. There is not, as on M^1, a cingulum crest or basin below this ridge, but the anterointernal cingulum is present, although minute. The external cingulum does cross the paracone, being widest here and developing a style external to the paracone (there is none anterior to the latter) and another, very indefinite, near the midpoint. The cingulum dies out on reaching the base of the metacone.

The diminutive M^3 is definitely quadrate, the crest from protocone to metacone being still more expanded and definitely angulate, with a

[1]It is noteworthy that mesostyles, in a topographic sense, may have at least two quite different origins. They may represent an outgrowth or angulation of the paracone-metacone crest, or ectoloph, or they may grow up on the margin of an external cingulum. In this animal both types of mesostyle are vaguely indicated.

tendency to form a vague cusp at the posterointernal angle. The protocone is completely anterior, without any basal cingula. The external cingulum is short and slight and bounds only a small median basin between paracone and metacone, which are still about equal.

As Matthew pointed out (1917) the only known mammals which this extraordinary form approaches at all closely are the more specialized members of the Phyllostomatidae, the subfamilies Sturnirinae, Stenoderminae, and Phyllonycterinae of Miller's classification. *Zanycteris* cannot be said to have any diagnostic characters of the Chiroptera as a whole. Indeed, its general habitus, as far as determinable, is definitely non-chiropteran, for instance in the anterior position of the zygomata, the marked constriction of the skull anterior to them, the relatively slender and elongate muzzle, and the weak, simple canines. The purely anteroposterior P^4, the great enlargement of M^1, and the post-canine diastema are not unknown among Chiroptera but are the exception rather than the rule in that Order. The loss of P^1 is highly characteristic of recent bats, but occurs in so many other orders that it is in no sense diagnostic.

The reference of *Zanycteris* to the Chiroptera depends, then, on a general, not very detailed resemblance of its molars to those of a few recent genera which are in this respect highly aberrant and the most specialized of all known members of the Order. The principal elements of this resemblance, every item of which is a distinction from primitive Chiroptera or from the Chiroptera in general, are:

Enlargement of M^1 (not, however, so marked in the recent genera in question).

Presence of a broad, shallow basin, tending to form a longitudinal valley.

Roughened enamel of basin.

Marginal position of cusps, their lack of distinctness, and the loss of the typical V-shape of the outer cusps of other Chiroptera.

Tendency to form a hypocone (or "pseudhypocone"[1]) by diversion and angulation of the protocone-metacone crest (but the hypocone does not arise this way in all the recent genera in question and may not in any, although it sometimes appears to).

The indication of affinities is not very convincing, and it is entirely possible that *Zanycteris* is not a chiropteran, but no other comparison can be suggested. If it is a bat, then it had already reached, or even in some details surpassed, the highest grade of aberrant specialization in the molars shown by recent bats, without (as far as shown) having acquired other chiropteran characteristics. It must be assumed, if it is

[1]A term which I find misleading and prefer not to employ, although it is rather deeply embedded in the literature.

considered chiropteran, to be especially related to the aberrant phyllostomatids, for if its characters do not indicate such highly special relationships they do not indicate chiropteran affinities at all.

With the very doubtful exception of a Lower Eocene specimen described by Cope, since lost, and really of unknown affinities, *Zanycteris* is the only supposed bat known from the Western Hemisphere before the Pleistocene, although it is, of course, certain *a priori* that the bats did occur here during the Tertiary.

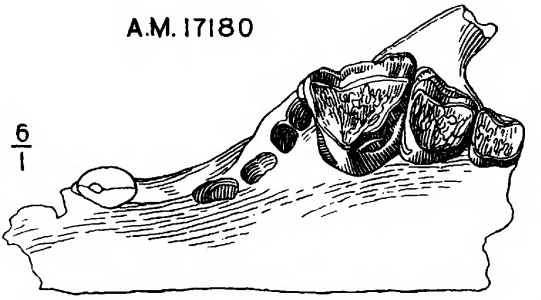

Fig. 6. *Zanycteris paleocena* Matthew. Type, Amer. Mus. No. 17180. Left upper jaw with M^{1-3}, with the canine (in outline) supplied from the right side of the same individual. Crown view. Enlarged six diameters.

Zanycteris paleocena Matthew, 1917[1]

Palaeonycteris paleocenica Weber and Abel, 1928 ('Die Säugetiere,' 2 Aufl. 2 Bd., p. 159), in error.

Type.—Amer. Mus. No. 17180, skull, very poorly preserved except most of palate, with right canine and M^{1-3} of both sides.

Horizon and Locality.—Mason Pocket, Tiffany Beds, Colorado.

Diagnosis.—Sole known species of genus as defined above. See also measurements below.

M^{1-3}.....4.2 mm.

C	M^1		M^2		M^3	
L	L	W	L	W	L	W
0.8	2.2	2.0	1.3	1.7	0.9	1.1

[1]The trivial name has hitherto been written "*paleocenus*" but is emended to agree in gender with the generic name. Νυκτερίς is feminine, and so are Latin nouns in *-ris*. It seems unjustified to consider *paleocenus* as one of the very exceptional Latin adjectives (e.g., *vetus*) with a feminine in *-us*. Within the spirit of the rules, such emendations are required and do not alter authorship.